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**Consistency of Skinner Box Activity Measures in
the Domestic Rabbit (*Oryctolagus Cuniculus*)**

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CONSISTENCY OF SKINNER BOX ACTIVITY MEASURES IN THE DOMESTIC RABBIT (*ORYCTOLAGUS CUNICULUS*)

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ABSTRACT: Consistency of individual differences in several measures of Skinner box operant and other activity and their intercorrelations in 14 chinchilla bred rabbits were studied. Reliability analysis revealed that both operant and activity measures were highly consistent (Cronbach alpha>0.87) over at least 15 days. Furthermore, locomotor activity, the tendencies to press the lever with high frequency, to make many errors, to check the presence of food in the dispenser as well as rearing were highly inter-correlated, making up a single dimension of activity. However, grooming did not correlate with these behaviors.

Individual differences in behavior are well known to everyone who works with animals of virtually any species. Some of the recent reviews (Budaev, 1997a; Clark & Ehlinger, 1987; Stevenson-Hinde, 1983; Wilson *et al.*, 1994) emphasized the importance of studying integrated behavioral phenotypes and stable traits that are consistent over time and across situations, that is, temperaments and personalities. The current evidence indicates (Budaev, 1997a,b; Royce, 1977) that two broad personality dimensions: Approach (Activity-Exploration), incorporating such traits as exploration, stimulus-seeking propensity and sociability; and Fear-Avoidance, composed of shyness, fearfulness, anxiety and escape, were systematically observed in various vertebrate species (ranging from fish to humans). This implies that common

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adaptive, neural and hormonal mechanisms may be involved. Defensive behavior, fear and general fearfulness have been particularly well studied (see Boissy, 1995 for a review). For example, Jones, Mills and Faure (1991) showed that various measures of fearfulness in chicks are not independent and all share the same underlying factor. On the other hand, the study of the second major temperamental trait, Activity, has attracted relatively less interest (but see Budaev, 1997b; Garcia-Sevilla, 1984; Goddard & Beilharz, 1984; Gomá & Tobeña, 1985; Maier, Vandenhoff & Crowne, 1988).

In the present research, the consistency of several measures of Skinner box activity and their intercorrelations in the chinchilla rabbit were investigated. While many people have studied the consistency and intercorrelations of various measures in the open field (e.g. Gomá & Tobeña, 1985; Maier *et al.*, 1988; Ossenkopp & Mazmanian, 1985; Ossenkopp, Sorenson & Mazmanian, 1994; Tachibana, 1985; see Archer, 1973, Walsh & Cummins, 1976 for reviews), it has been suggested (Hirsch, 1962) that "Skinner developed apparatus which affords probably the most reliable measure of individual differences ever obtained in the laboratory" (p. 6), due to the fact that very lengthy tests are possible. It has been found (Reed & Pizzimenti, 1995) that in four learning tasks involving response inhibition, rats' performance was consistent over time (but not across tasks). In addition, within the behavioristic framework, operant measures have proved to be very appropriate for the study of human personality and adjustment (see Harzem, 1984).

METHOD

Subjects

The animals were 14 male chinchilla bred rabbits (*Oryctolagus cuniculus*) approximately 3-4 months of age weighting 1.6-2.0 kg. They were obtained from a local supplier. During the present study the animals were maintained in standard individual cages 43 x 65 x 40 cm. The temperature was held constant $19 \pm 1^\circ\text{C}$ and the light-dark cycle was 12:12 h.

Procedure

Each individual was initially trained to press the lever to obtain

food in a single Skinner box: a metal grid box 65 x 85 x 85 cm with wooden floor and a single flat plastic lever 10 x 19 x 3 cm mounted 3 cm above the floor level. Both the maintenance cages and the Skinner box were situated in a single room and lit by four 60-100 W bulbs suspended 3.5 m above them. The rabbits were given a laboratory rodent chow (140 g per day). Prior to the first training session they were food-deprived for 24 hours and in the further sessions we reduced their daily ration to 1/2 of the normal. Every training and test session took place from 10:00 to 14:00 hr and was continued for 60 min. Immediately after the animal pressed the lever, a piece of carrot (0.5 g) appeared in the food dispenser at the opposite side of the box. A continuous reinforcement schedule (FR1) was used. The Skinner box was washed and cleaned with 96% alcohol after each training session. All individuals were rather easy to train in this apparatus and after a maximum of 3-4 days of training they reached the criterion of receiving a minimum of 40 carrot pieces within a 60 min. period, which corresponded to at least 10 consecutive responses without error. All training sessions were performed in presence of the observer and the rabbits were handled. This was necessary to minimize possible fear in subsequent test sessions and accustom animals to the presence of the observer.

Two-three days after a rabbit reached the criterion, he was placed into the same Skinner box for 60 min. for testing. A single observer (SVZ) recorded the following behavioral measures: (1) the number of presses of the lever; (2) the number of food pieces eaten (on some occasions the rabbits could press several times in succession, for which they were reinforced by only one food piece); (3) the frequency of errors, when the rabbit approached the lever but missed it or did not press, but went to the food dispenser and checked it for food; (4) checking the food dispenser, by approaching it and pushing his nose into it without having pressed the lever previously; (5) the frequency of rearing; (6) gross locomotor activity, that is the frequency of any movements (any horizontal activity like walking, jumping etc.) inside the Skinner box not related to the lever-pressing behavior, feeding or checking the food dispenser (the behaviors were counted as distinct units only if they were separated by other behaviors or stops); (7) the frequency of grooming (e.g. scratching, washing, licking; each unit typically lasted for up to 5 s). This test was administered five times to each individual rabbit with three days between test intervals.

RESULTS AND DISCUSSION

First of all, the distribution of each of the 35 behavioral variables (7 behaviors x 5 test sessions) obtained were analysed. Because of small sample size ($N = 14$), the influence of any deviation from normal unimodal distribution or an excessive skewness would have had a large detrimental effect and even a single outlier may have been very influential. However, inspection of the normal probability plots for each variable revealed no outliers in the data and the distributions approached normal in all cases. Thus, it was justified to apply parametric statistical methods to the data analysis.

A one-way repeated measures ANOVA was performed to test for possible changes in the mean values of the behavioral measures over the five test administrations. With only one exception, locomotion, the differences turned out not to be significant (see Table 1; even in the case of locomotion, the differences between test sessions accounted for only 2.13% of variance and no linear trend was pronounced – contrast analysis, $F(1, 13) = 3.06$, $p = 0.103$; means over days were 30.8, 32.8, 40.8, 31.1, 43.0). This clearly indicates that the rabbits were well trained and no further improvement in learning took place.

Table 1. Between-trial changes in the behavioral measures (repeated measures ANOVA) and their consistency across repeated trials, $N=14$.

Behavioral measure		Between-trial ANOVA		Cronbach alpha
		$F(4, 52)$	p	
1	Lever-presses	1.23	0.31	0.90
2	Food pieces eaten	1.11	0.37	0.92
3	Errors	1.68	0.17	0.95
4	Checking the food dispenser	0.37	0.83	0.87
5	Rearing	0.49	0.74	0.91
6	Locomotion	2.75	0.04	0.97
7	Grooming	2.05	0.10	0.93

To see to what extent the behavioral measures were consistent over the five test administrations, a reliability analysis was performed. First, for each variable, the correlations between all test sessions were computed and, second, on the basis of the resulting pairwise correlation matrices, Cronbach alpha coefficients were inferred (Nunnally, 1967). All pairwise correlations turned out to be high and significant ($p < 0.05$), so that the alpha coefficients were also remarkably high

(Table 1). In other words, the behavioral measurements were fairly reliable and the rabbits were extremely consistent and repeatable in their behavior for at least 15 days. This allowed the scores over the test sessions to be aggregated to further diminish the contribution of unique environmental variance and measurement error (Ossenkopp & Mazmanian, 1985; Tachibana, 1985). Thus, 35 original scores were collapsed to only 7 summary measures, one for each behavior unit.

In addition, two indices were computed which measured the relative number of errors adjusted for the overall operant performance, that is, the frequency of errors divided by either the number of lever presses and the number of food pieces eaten. Both proved to be also very consistent (both alpha coefficients are 0.92), stable over repeated test sessions (repeated measures ANOVA, both $p > 0.1$) and correlated closely with the overall error frequency (correlations between aggregated scores are, respectively, 0.89 and 0.85). Thus, being redundant, the indices of relative frequency of errors were not included in the subsequent principal component analysis.

Table 2. Intercorrelations between the behavioral measures (the correlation matrix). With $N=14$, correlations greater than 0.53 are significant at $p < 0.05$ (shown in bold type).

Behavioral measure	1	2	3	4	5	6	7
1 Lever-presses	1.00	.99	.61	.56	.76	.79	-.17
2 Food pieces eaten	.99	1.00	.63	.58	.77	.82	-.19
3 Errors	.61	.63	1.00	.67	.53	.56	.09
4 Checking food dispenser	.56	.58	.67	1.00	.80	.78	.34
5 Rearing	.76	.77	.53	.80	1.00	.92	.07
6 Locomotion	.79	.82	.56	.78	.92	1.00	.13
7 Grooming	-.17	-.19	.09	.34	.07	.13	1.00

The aggregated variables were intercorrelated and further subjected to the principal component analysis (Nunnally, 1967). All behavioral measures, except grooming (it correlated with no one other behavior, $r < 0.34$, $N = 14$, $p > 0.23$), proved to be significantly and positively correlated (Table 2) with one another (it is worth noting that the rearing frequency was highly correlated with the locomotion). We also computed the Bartlett sphericity test, Kaiser-Meyer-Olkin measure of sampling adequacy and inspected off-diagonal elements of the anti-image covariance matrix (Dziuban & Shirkey, 1974). They indicated that the correlation matrix was appropriate for the principal component

analysis (Bartlett's test: $\chi^2 = 110.4$, $df = 21$, $p < 0.001$; Kaiser-Meyer-Olkin measure of sampling adequacy = 0.61; only 9.5% of all anti-image covariances exceeded the conventional cut-off value of 0.09). Two principal components with the eigenvalues greater than unity were extracted, which accounted for 84.6% of the total variance. The maximum residual correlation was only 0.16 (the maximum value acceptable with $N = 14$ is 0.26), further indicating that the component solution was quite satisfactory. All variables but grooming had salient loadings on the first component (see Table 3).

Table 3. The pattern of intercorrelations between the behavioral measures: Varimax rotated principal components (PC); salient loadings (>0.7) are given in bold type.

Behavioral measure	PC 1	PC 2
1 Lever-presses	0.92	-0.27
2 Food pieces eaten	0.93	-0.27
3 Errors	0.74	0.14
4 Checking the food dispenser	0.81	0.46
5 Rearing	0.91	0.12
6 Locomotion	0.93	0.14
7 Grooming	0.00	0.95
Eigenvalue	4.62	1.30
Variance accounted for (%)	66.07	18.50

These results clearly indicated that in the present operant situation, individual rabbits differ primarily along a single and quite stable dimension. This trait encompasses such behaviors as horizontal locomotion, tendency to press lever with high rate, to make many errors, to check food in the dispenser frequently, as well as rearing. Furthermore, rearing is typically considered a sort of exploratory behavior (Gomá & Tobeña, 1985; Walsh & Cummins, 1976), extraversion (Garcia-Sevilla, 1984) and excitability (Lát & Gollová-Hemon, 1969) in various rodents and consistently correlates with locomotion (Gomá & Tobeña, 1985; Maier *et al.*, 1988; Ossenkopp *et al.*, 1994; Tachibana, 1985; Walsh & Cummins, 1976) as well as with the caloric intake per surface area (Lát & Gollová-Hemon, 1969). In rabbits, rearing in the open field test was found (Meijsser *et al.*, 1989) to correlate with locomotion and exploration. Accordingly, this continuum distinguishes animals from "dull", inactive and careful to active, exploratory and "careless".

Thus, even though little can be said about the generality of this dimension across situations (e.g. see Reed & Pizzimenti, 1995 for a report of no consistency across situations requiring response inhibition), it seems reasonable to suppose that it might be related to general activity, sensation seeking and susceptibility to reward. As such, this dimension may be mediated by certain neurotransmitters, most probably dopamine, which is implicated in various natural (food, water) and unnatural (drugs, intracranial self-stimulation) rewards, exploratory behavior, positive affect and the extraversion personality trait (Wise & Rompre, 1989; Zuckerman, 1994). This would be a perspective topic of a future study.

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OBSERVING BEHAVIORAL QUALITIES

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ABSTRACT: Animal movements have distinctive qualities, and these qualities can vary even when the form of the movement remains relatively constant. Description of behavioral qualities by trained observers can be useful in basic behavioral research and in applications ranging from behavioral ecology to clinical medicine. A method called Laban movement analysis differentiates four separate bipolar effort factors that contribute to the quality of body movement. Using independent rankings of videotaped behavioral sequences, we verified that observers can distinguish behavioral qualities reliably when using the Laban system. Observers generally agreed both on the kind(s) of effort factor(s) present and on the mode or degree of expression of each factor. We discuss the potential and limitations of the Laban system as applied to animal behavior and identify some philosophical issues that arise from attempts to link the study of behavioral quality to the study of form and space, and to a possible emerging "science of qualities".

Qualities of behavior vary in nature. A familiar individual's distinctive walk is recognizable at a distance, long before facial features or body markings become evident. A primate mother might reject her infant by pushing it away roughly or by pushing it away gently. Play behaviors in young and adult animals also appear to have distinct qualities. For example, play-gaits in rhesus macaques (*Macaca mulatta*) (Sade, 1973) and in other species (Fagen, 1981, p. 415) have a bouncy or gamboling quality. Observers of play report relaxed muscle tone (Aldis, 1975), lightness and lack of tenseness (Kaufman & Rosenblum, 1966), and exaggeration of individual movements (Loizos, 1966).

Qualities of an action must be appropriate to that action's goal. Precise painting with a brush and shaking paint off the same brush are actions having similar forms, different qualities, and different effects and functions. Hands may clap in anger or in delight -- the same gesture, expressive in different ways through contrasting qualities.

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Behavioral qualities are important for efficiency and expressiveness of functional behavior. Furthermore, an observer's pre-existing perceptual biases may make the qualities of a particular action attractive to that observer even though this action lacks direct biological function. For all these reasons, it is interesting to try to observe behavioral qualities (the "how" of behavior) reliably.

Pioneering observers of behavior noticed behavioral qualities and clearly sensed that these qualities were important for addressing the questions or phenomena under study. Ecologist Robert MacArthur (1958) informally contrasted the "nervous" foraging movements of the black-throated green warbler *Dendroica virens* with the "deliberate" feeding habits of the bay-breasted warbler *D. castanea*. Clinician and writer Oliver Sacks (1987) summarized classic signs of Parkinsonism including quick, abrupt, and brief movements ("festination" and "pulsion").

Formal methods for describing behavioral qualities are little-known, and scientists have not previously considered using such tools in their work. Laban movement analysis (Bartenieff, 1980; Dell, 1977; Laban & Lawrence, 1974; Moore & Yamamoto, 1988) is a long-established method for studying the form and qualities of movement. We hypothesized that it would furnish a reliable approach to qualities of nonhuman behaviors. Levy (1990) used Laban methods in an exploratory study of confined, trained Atlantic bottlenose dolphins *Tursiops truncatus* and their trainers. Zhou and Shirley (1997) included Laban terminology in their description of red king crab *Paralithodes camtschaticus* locomotion. Neither study measured interobserver reliability.

Laban and his successors analyzed movement in terms of Body, Effort, Space and Shape elements. Effort analysis specifically addresses dynamic qualities of body movement. The other three elements can contribute in various ways to expressive movement but do not address movement dynamics *per se*. The term "body" refers to initiation and sequencing of movements, and body parts involved in movement. "Space" defines different kinds of spatial pathways that an actively moving body can take. "Shape" defines ways in which the body forms itself in space.

METHOD

We used Laban Effort methods to observe animal behavior. Laban

Effort analysis identifies four motion factors for identifying specific qualities or dynamics of movement. These factors are Space, Time, Weight, and Flow. Each factor represents two contrasting ways or modes of expression in which muscular effort can produce movement.

Space can be direct or indirect. Direct space effort is channeled in a particular spatial direction or focused on one point in space. Indirect space effort is expansive and multifocal. For example, a cat may focus all its energy and attention in one direction as it intently watches a mouse hole (direct). A bear may stand bipedally, looking and sniffing around as it seeks to localize the source of an odor or sound (indirect).

Time can be quick or sustained. Quick time effort produces acceleration or condensing of time with movements that appear rushed or hurried. Sustained time effort delays and decelerates movement. A stalking cat's movements are sustained until the final, quick spring on the prey.

Weight can be strong or light. Strong weight effort appears when pressure is applied forcefully during movement. Light weight effort involves a decrease in applied pressure so that the movement is not forceful. A bear may use all of its weight when digging for plant roots (strong). Or it may handle a gravid female salmon very delicately to extract the roe, a preferred food (light).

Flow can be bound or free. Bound flow effort serves to control and restrict movement. Free flow produces easy, unrestrained movement (free). A barefoot child may walk carefully across a stony beach (bound) to run and splash with abandon in the water, arms and legs swinging in all directions as the inertia of the movement is allowed to take over (free).

In Laban's work, the four elements Body, Effort, Shape and Space are connected. However, each element may be examined individually (Andrews & Scott 1986). We chose to concentrate on Effort while recognizing that additional insights and accuracy regarding behavioral quality may result from use of additional elements of the full Laban system, particularly Shape, to analyze behavior.

Methods used here to study behavioral qualities address the "how" of behavior. Form and position of movement, by contrast, constitute the "what" of behavior. Precise methods for the study of form and position include Eshkol-Wachmann notation (Golani, 1992) and aspects of Labanotation (Hutchinson, 1970). Eshkol-Wachmann and Labanotation methods differ (Bartenieff, 1980; Horwitz, 1988). Neither method addresses behavioral quality.

Procedure

We investigated reliability of Laban analysis for behavioral quality, using two observers in a laboratory setting. Both observers were biology students in the senior author's introductory one-semester (2 h/wk for 16 wk) Laban analysis workshop. Neither student was a professional dancer or college dance major. The scoring session whose results are reported here took place at the end of the workshop.

Observers analyzed eighteen independent, non-contiguous segments of six videotapes (three segments per tape) showing behavior of nonhuman animals in naturalistic settings. No tape previously shown in the workshop was analyzed in these tests. Additional criteria for choosing test tapes were that (1) the technical quality of the video recording had to be adequate for analysis, (2) each tape had to be of a different nonhuman species, (3) no portion of any test tape had been analyzed previously in terms of movement qualities, (4) the segments analyzed should show animals moving on or from a solid substrate rather than in a fluid medium, and (5) extremely small and extremely large animals (relative to humans) were not included in this initial study because time, weight and space scales for movement in animals whose body size differs from that of humans by many orders of magnitude are relative and may require special study techniques, correction factors or methods of analysis.

We used the first six tapes that met all these criteria. Species and activities analyzed included one primate (*Gorilla gorilla* travel and social behavior), four carnivores (*Canis familiaris* bounding, object handling and vigilance, *Panthera pardus* pouncing and pawing, *Panthera tigris* travel, *Ursus arctos* jumping, prey handling play and locomotor play), two ungulates (*Capra ibex* social contact and travel, *Rupicapra rupicapra* pawing), and one bird (*Pica pica* displacement, travel and vertical movement). 1/2 inch Super Beta format tapes were played on a SONY SL-340 video machine and viewed on an 18-inch SONY KX-1901 monitor. Both observers watched and then scored each tape segment simultaneously. Observers were given as much time and as many repetitions as they needed to score each segment before going on to the next. Observers were not allowed to communicate with one another or to discuss their observations or conclusions until after all scores had been recorded for the entire session. Observers scored each segment independently of one another for the Laban motion factors Space (direct or indirect), Time (quick or sustained), Weight (strong or light), and Flow (bound or free). If one or more factors were absent then the segment was scored as "absent" for that factor or factors. For

example, the first observer scored the first segment on the first videotape as indirect Space and quick Time, with Weight and Flow both absent.

Our primary measure of agreement between observers was Kendall's (1975, p. 45-48) measure of association in a contingency table with ordered categories. Kendall's measure is preferable to kappa coefficients (Landis & Koch, 1977) because Kendall's measure recognizes the ordering of modes of expression on each motion factor, whereas kappa does not. We also calculated kappa coefficients because they are more familiar to most students of behavior. The terms "fair", "moderate", "substantial" applied in this paper and elsewhere to kappa coefficients are arbitrary and refer to the intervals 0.21-0.40, 0.41-0.60, and 0.61-0.80 respectively (Landis & Koch, 1977, p. 165). No "magic figure" exists beyond which a behavioral measure is accepted as reliable (Martin & Bateson, 1986, p. 91). Important but difficult-to-measure categories with fair to moderate kappa coefficients can still be useful (e.g., Smith & Vollstedt, 1985). Correlations are not appropriate for measuring reliability in this particular study because data are categorical (nominal) rather than ordinal or interval.

Observers' responses could differ in kind and/or in degree. We say that responses differ in kind when both observers notice the presence of the same behavior quality factor but disagree about its mode of expression. For example, suppose that both observers noticed the presence of Flow, but one observer recorded bound Flow, the other free Flow in the same movement or movement sequence. In this case, the observers' responses would be said to differ in kind. But what if one observer noticed Flow (bound or free) but the other saw no Flow quality and scored Flow as absent in the same movement or movement sequence? In this case, we would say that the responses differed in degree. One observer considered Flow to be present and the other observer viewed it as absent. To analyze degree and kind separately, we calculated separate reliability coefficients for these two components of observer response (illustrative numerical example, Table 1).

We felt that two reliable observers would very seldom differ in kind. Both would usually agree that they saw the same mode of expression for Flow (for example), if intense Flow was truly present. One would not see bound Flow and the other see free Flow in the very same movement. We also realized that observers might sometimes disagree about presence or absence of a particular behavior quality. All factors of movement quality can occur to some degree in actual movements, and advanced Laban movement analysis distinguishes

different levels or intensities of expression of a given factor (Dell, 1977, p. 12, 32). (See Appendix for further explanation).

Note that when agreement in kind is analyzed for eighteen video segments, the total number of agreements/disagreements for analysis will be less than or equal to eighteen because we are only considering those cases in which both observers scored a particular factor as present. For example, in Table 1 there were four cases in which at least one observer scored a particular factor as absent, leaving fourteen cases for analysis of agreement in kind.

Table 1. Illustrative Data from Two Observers, Analyzed in Terms of Agreement in Kind and Agreement in Degree. Abbreviations: I = indirect spatial focus; D = direct spatial focus; Y = present; N = absent.

		Observer 1								
		Original Data			Kind			Degree		
		I	-	D	I	-	D	Y	N	
Observer 2	I	2	0	1	2	-	1	Y	13	1
	-	1	1	2	-	1	-	N	3	1
	D	1	1	9	1	-	9			

We did not test interobserver reliability coefficients for statistical significance. Level of statistical significance of a reliability coefficient says little about the actual degree of reliability (Martin & Bateson, 1986, p. 91).

RESULTS

Interobserver agreement on each factor was positive and fair to moderate for both measures (Table 2). Agreement in kind was positive, moderate to perfect, and stronger than agreement in degree (Table 3) for Time, Weight, and Space. For Flow, agreement in kind was moderate and agreement in degree was substantial.

Agreement in degree involves measures that allow data from different effort qualities to be combined. The number of observations in the combined sample is sufficiently large to allow G-squared tests of interobserver reliability (Fienberg, 1980). A hierarchical log-linear model in which the two observers' assessments of degree were associated, but independent of tape number, was the simplest model needed to fit the data (Table 4) adequately (G-squared = 20.4, $df = 15$, $p = 0.16$).

Table 2. Observer Ratings and Reliability. Abbreviations: I, indirect; D, direct; S, sustained; Q, quick; L, light; H, strong; B, bound; F, free.

Observer 1																
Space					Time				Weight				Flow			
I - D					S - Q				L - H				B - F			
Observer 2	I	2	0	1	S	2	2	0	L	3	4	0	B	4	1	2
	-	1	1	2	-	3	3	1	-	1	6	1	-	0	2	0
	D	1	1	9	Q	2	1	4	H	0	1	2	F	2	0	7
Kendall		.45			.34			.46			.44					
Kappa		.38			.27			.37			.54					

Table 3. Kappa Coefficients for Agreement in Kind and in Degree

Source of Agreement	Factor			
	Space	Time	Weight	Flow
Kind	0.56	0.50	1.00	0.44
Degree	0.15	0.24	0.22	0.77

Table 4. Three-Way Contingency Table for Reliability Analysis (Degree Only). Variable 1, rating of observer 1; variable 2, rating of observer 2; variable 3, tape number.

		Observer 1											
		Tape 1		Tape 2		Tape 3		Tape 4		Tape 5		Tape 6	
		Y	N	Y	N	Y	N	Y	N	Y	N	Y	N
Observer 2	Y	7	0	7	1	6	2	8	4	7	1	6	2
	N	1	4	1	3	3	1	0	0	1	3	3	1

The non-significant P in this test means that the model fits the data (lack of fit not significant). A second model assuming no association among the three variables did not fit the data (G-squared = 29.8, df = 16, $p = 0.02$). Fits of the first and second models differed significantly (G-squared = 9.4, df = 1, $p < 0.005$). Interaction terms involving tape number did not improve the fit significantly when added to the first model.

Separate analyses of agreement in kind for each effort quality were not possible for reasons of sample size. However, Laban theory identifies indirect, sustained, light and free as "indulging" qualities and direct, quick, strong and bound as "fighting" or "resisting" qualities (Bartenieff, 1980, p. 51; Moore & Yamamoto, 1988, p. 157). We used this identification to construct a combined sample (Table 5), including all data and measuring both agreement in kind and agreement in degree.

Table 5. Three-Way Contingency Table for Reliability Analysis (overall). Abbreviations: I, indulging; F, fighting. Variable 1, rating of observer 1; variable 2, rating of observer 2; variable 3, tape number.

		Observer 1																	
		Tape 1			Tape 2			Tape 3			Tape 4			Tape 5			Tape 6		
		I	-	F	I	-	F	I	-	F	I	-	F	I	-	F	I	-	F
Observer 2	I	4	0	0	3	1	1	2	2	1	1	2	1	4	1	1	1	0	0
	-	0	4	1	1	3	0	2	1	1	0	0	0	1	3	0	1	1	2
	F	0	0	3	0	0	3	0	0	3	1	2	5	1	0	1	0	2	5

A hierarchical log-linear model in which the two observers' assessments were associated, but independent of tape number, was the simplest model needed to fit the data adequately ($G\text{-squared} = 48.1$, $df = 40$, $p = 0.18$). A second model assuming no association among the three variables did not fit the data ($G\text{-squared} = 81.4$, $df = 44$, $p < 0.001$). Fits of the first and second models differed significantly ($G\text{-squared} = 33.3$, $df = 1$, $p < 0.0001$). Interaction terms involving tape number did not improve fit significantly when added to the first model. Expectations were smaller than ideally required (48 of 54 were 0.67 or greater, 24 of 54 were 1.00 or greater). Expectations for the analysis of degree in kind would have been even smaller, so this analysis was not done.

DISCUSSION

Mastery of Laban analysis can require several years of full-time study. But the Laban techniques investigated here appear reliable when applied to animal behavior even by relatively inexperienced observers. When observers agreed that a particular factor was present, they generally agreed on its mode of expression.

To model the stream of ongoing behavior with a sequence of discrete patterns that are fixed in form and that vary only in frequency, duration and intensity (Fagen & Young, 1978) is to ignore qualitative aspects that a perceptive observer might well notice and consider important. The study of behavior can include both direct, objective data on acts in sequence and reliable descriptions of qualities that we notice in everyday life (cf. Feaver, Mendl, & Bateson, 1986; Hinde, 1976).

Subtle differences in movement qualities can determine how well one species does relative to another in a particular habitat. Predator avoidance is one component of such success, and ecological studies of vigilance behavior might productively distinguish between direct and indirect spatial effort by a vigilant animal. Behavioral qualities could play a role in ritualization, in perceptual movement cues, and in dynamic traits of visual communication, e.g. in studies of sexual selection and prey-predator interaction. Qualitative measures of drug effects in behavioral pharmacology could use Laban techniques as a novel exploratory tool. Behavioral qualities defined by Laban methods could help define individual distinctiveness. Laban methods may also prove useful in defining and measuring qualities of animal play.

Highly-skilled Laban observers can readily distinguish varying degrees of intensity along the axis of each effort quality. For example, one observer may score a movement as weakly Light, whereas another might score the same movement as weakly Strong. This pair of scores would have been analyzed as a failure to agree in degree, but would actually reflect a higher level of concordance than would occur from a complete disagreement in degree (very Light vs. very Strong). Because this study involved trained but not expert observers, we chose not to differentiate the scale of observation so finely. Had we been prepared to score degrees of intensity along each effort gradient, the resulting agreement in degree might actually have been higher than that reported here.

We were all trained by the same Laban teachers, but different schools of Laban studies exist and observers who have learned Laban techniques differently may not agree as well as we did. Our impression is that the differences between these schools involve matters of emphasis (of Effort versus Shape, for example) or simply of terminology.

The Laban approach has other obvious limits as well. Additional dimensions or sets of dimensions may prove fruitful for defining qualities of animal behavior. Problems of interpretation may confront analyses of very small and very large animals, and of animal movement in fluid media.

In Laban studies, observations of Effort are closely linked with observations of Shape, "how the body forms itself in space" (Dell, 1977, p. 43). Effort qualities are said to be easier to observe accurately when the observer also records Shape dynamics. This aspect of Laban methods merits consideration for future studies of behavioral quality.

Laban methods require a preliminary training period involving active movement by the prospective observers and motor learning of each relevant quality and concept. In general, can training programs that include active movement in a structured, systematic context actually help humans learn to observe animal behavior more reliably? This hypothesis deserves empirical investigation.

Laban methods have been applied to the study of dance and human movement across many cultures, but these methods may include language-specific or culture-specific features. Although Laban's concepts have successfully survived translation from German to English, it would be worthwhile to see just what native speakers of other languages, particularly non-Western languages, might offer regarding concepts and terms for movement quality. Valuable both in its own right and as an exercise in cross-cultural extension of the approach would be a study that compiles lists of qualitative traits and then determines reliability of these traits in a controlled manner (e.g., Fagen & Fagen, 1996; Feaver, Mendl, & Bateson, 1986). One or more individuals familiar with the animals selects a list of items that reflect a broad range of the types of behavioral qualities that occur under the conditions of observation. These items are then ranked by independent observers and the rankings compared statistically using nonparametric correlation methods.

The philosophical concepts of form, quality, and space play key roles in scientific theory and practice, as well as in the philosophy and making of art. Western concert dance, for example, admits a clear distinction between the form of a dance step from the classical syllabus and the various expressive qualities with which it can be performed. Analogous issues arise in music performance. A musical score can indicate both the notes to be played and the expressive quality intended by the composer. Expansive biological discussions of form, quality and space can also furnish grist for the philosopher's mill, as the following examples may indicate.

Goodwin (1996, p. 196-8) predicts that "a science of qualities" will emerge from the study of biological form (both spatial form, e.g. the shape of a salamander body, and temporal form, e.g. "the distinctive flight of a woodpecker"). Woodpeckers' undulating flight is indeed distinctive (Peterson 1980, p. 188). "Distinctive" here seems to imply

the form of the spatial path traced by the bird's movements, but flying or any sort of locomotion will generally involve effort qualities as well. Laban sought to relate dynamics or qualities of movement to qualities of form as expressed in shape, in space, and in the moving body's dynamics of muscular exertion or effort.

Concepts of design (e.g., Smith 1981, Stevens 1974) endure in discussions of biological form and natural pattern. Haeckel coined the term "ecology" from the Greek *oikos*, "house". Grinnell named and defined the ecological niche. Architectural spandrels (Gould & Lewontin, 1979; Gould, 1997) inspire evolutionary ideas. Schwenk (1976) viewed form as the visible manifestation of dynamic processes, and especially of hydrodynamics. Organisms "express their natures through the particular qualities of their form in space and time" (Goodwin 1996, p. 198). Is it meaningful to suppose that ways of thinking intrinsic to a science of qualities might resemble ways that designers of all persuasions, from architects to choreographers, work and play with qualities of form in space and time?

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APPENDIX

Measuring Separate Components of Agreement with Kappa

1. *Agreement in kind.* To calculate a kappa coefficient that measured observers' agreement on the mode of expression of Flow (for example), given that both observers agreed on the presence or absence of Flow in the movement, we calculated expected values for a 3x3 table that had structural zeroes in the four cells (1,2), (2,1), (2,3), (3,2) where exactly one observer scored the Flow as absent. This arrangement of structural zeroes ensured that expected values only contributed to kappa when observers agreed that Flow was present, or when they agreed that Flow was absent. We made these calculations with the `loglin()` function in S-Plus for Windows, version 3.3 (StatSci Division, MathSoft Inc., Seattle, Washington, USA), which implements iterative proportional fitting methods for incomplete contingency tables (Fienberg, 1980).

2. *Agreement in degree.* To calculate a kappa coefficient that measured observers' agreement on the presence or absence of a particular motion factor, we calculated expected values for a 2x2 table constructed as follows. For the upper left-hand corner of the table, cell (1,1), we counted all cases in which observers agreed that Flow (for example) was present. For the lower right-hand corner of the table, cell (2,2), we counted all the cases in which observers agreed that Flow was absent. Off-diagonal cells contained the counts of cases in which one observer saw Flow and the other did not.

EVOLUTIONARY PSYCHOLOGY, ADAPTATION, AND THE EVOLUTION OF LANGUAGE: IS THERE A NEED FOR COMPARISON?

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ABSTRACT: A general assumption held by evolutionary psychologists is that a reference point for examining the origins and evolution of human psychological adaptations exists within a time range beginning roughly two million years ago. Scenarios for explaining the evolution of human psychological processes often allude to possible selection pressures encountered by hominids during this time. Unfortunately, comparative psychology and ethology are relatively absent from much current evolutionary psychological thought. Selective pressures that existed during the putative environment of evolutionary adaptedness may have predated the origin of hominids. Based on examples of the evolution of communication, this paper offers another approach to discovering the origins and evolution of psychological traits, with the aim of modifying a potentially misleading assumption of evolutionary psychology.

"The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind" (Darwin, 1871, p. 128).

Comparative psychology has confirmed Darwin's assertion in so many ways. The mental differences among humans and the "higher animals" are largely of degree, although some evolutionary discontinuities exist for which we may never find capacities, rudiments, or vestiges in other species. Despite some of its historically limited focus (Beach, 1950), comparative psychology is at a theoretical advantage over many other fields of psychology by virtue of its relationship to evolutionary theory. Evolutionary psychology is a relatively recent attempt to synthesize evolutionary biology with the

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theoretically bereft field of psychology [see Tobach (1995) for a historical discussion of both evolutionary and comparative psychology]. Psychology as a whole is not woven together with a general theory such as natural selection, which, since its inception, has united most of the various subfields within the biological sciences. As Buss (1995) stated "...psychologists assume that the human mind is a whole and integrated unity, no metatheory subsumes, integrates, unites, or connects the disparate pieces psychologists gauge with their differing calipers " (p. 1).

Although Darwinian thought has often been applied to human behavior, it has not brought the field of psychology together across all of its subdisciplines. The chance that some natural theory applies only to humans is vanishingly small. Thus human behavior, in all of its complexity, should be explicable in evolutionary terms. Specifically, natural selection could serve as a metatheory that unites psychology, which would not necessarily alter the sub-theories that are currently scattered across the discipline, but could possibly increase (or constrain) their explanatory power.

Evolutionary psychologists often remind us that our current suite of behavioral characters evolved under conditions quite different from those of the present day, and that an ancient point of reference is needed wherein original selective pressures can be considered. By embracing natural selection as a unifying theory, evolutionary psychologists present themselves with two general questions; namely, what is the historical origin of the trait in question and what is its function? These questions are generally answered using the concepts of an "environment of evolutionary adaptedness" (EEA), and "adaptationism". Specifically, the EEA was the setting in which the human evolutionary drama was played out during the Pleistocene epoch. Most humans have dispersed and rapidly altered their surroundings to degrees that render them virtually incomparable to regions inhabited during the EEA. However, behavioral patterns and thought processes that were adaptive during this time period (and the settings therein) remain firmly embedded in human psychology.

There is often a link between the historical origin and function of a trait, but, according to many, the two should be recognized as potentially separate (e.g., Gould, 1991; Gould & Lewontin, 1979). This topic has a long history of debate within the biological sciences [see Allen, Bekoff, and Lauder (1998) for a compilation of various perspectives on adaptationism]. Although adaptationism is an important concept for evolutionary psychology, the focus of this paper is less on

the concept of adaptationism itself, and more on pinpointing the origins of the putative adaptations hypothesized by evolutionary psychologists.

THE MODULAR MIND

The brain, like any other bodily system, is material that is altered via natural selection. The pervasive influence this has on behavior is obvious. However, an appropriate model for brain architecture is required, as an understanding of the brain remains vague in comparison to other bodily systems. Evolutionary psychologists have adopted Fodor's (1983) "modular" model of the brain. Generally, the architecture of a modular brain consists of discrete neural units whose functions are fairly specific; and although the topographical layout of these units may be scattered throughout the brain, their manifest behavior and thought patterns are much less diffuse. That is, they are "domain specific", which contrasts with an alternative view that the brain as a whole is relatively unconstrained and remains relatively free to adapt to individual circumstances. The development of the modular brain model fits with a shift from the view that psychology must limit its focus to measurements of stimulus input and behavioral output, to a cognitive perspective. Tooby and Cosmides' (1992) review of the past century of social science in general shows that a new model of the mind, as well as an increasing appreciation for the role of biological processes in behavior, represent a backdrop for an evolutionary psychology.

FITNESS GOALS AND ADAPTATIONISM

One noteworthy point of departure taken by evolutionary psychologists from say, sociobiologists, is the moderate stance taken on fitness "goals". Rather than view humans as "fitness strivers", evolutionary psychologists such as Tooby and Cosmides (1990) propose the terms "adaptation executors" and "mechanism activators" as more appropriate descriptors. These terms integrate the modular and adaptationist perspectives into the conceptual framework of the field. Modern day human activities such as consuming fatty foods and smoking are not suggestive of a fitness-maximizing organism, and viewing pornography is a reproductive dead end. Buss (1995) maintains that such non-fitness promoting tendencies are products of evolved mechanisms from ancestral humans, and the conditions that elicited

them in ancestral humans fundamentally differ from those of modern day humans. According to Buss (1995), to suppose otherwise is to commit the "sociobiological fallacy", which confuses the nature of the psychological mechanisms employed by modern humans with their historical origins.

Among the problems of proposing adaptive explanations concerns the difficulty in testing what a given trait is adapted for. Because the EEA is not repeatable, difficulties arise in testing hypotheses of the historical origins of human cognitive processes. This difficulty, of course, is not unique to this situation but pervades evolutionary biology in general. The current utility of psychological traits may have their origins in other traits, or may be byproducts of a combination of other traits. Also, the EEA concept implies that the origins of much of human cognition arose during a specific period. This may be true for much of human cognition, but findings in comparative psychology and ethology suggest that the historical origins of many human behaviors have their beginnings in times predating the Pleistocene. Thus the selective factors involved in the evolution of human cognitive adaptations, or at least the foundations upon which they were built, may not be the same as some of those hypothesized by evolutionary psychologists, or, if certain selective pressures were relatively constant, they may have predated the Pleistocene. This potential problem can be illustrated by using examples from the evolution of language.

THE "LANGUAGE INSTINCT"

The evolution of language is a topic of great interest to evolutionary psychologists (Bickerton, 1998; Pinker & Bloom, 1992). Human languages differ in some important ways from the communication systems evolved in other species. The human brain has expanded and reorganized considerably through the hominid lineage, and the capacity to acquire a symbolic language evolved to its current state of complexity during this period (Deacon, 1997). The specific selective factors that shaped human language have proven difficult to identify. The Australopithecines probably did not speak, as their brains were not much larger than the brains of modern day apes. However, over a 2-million year period, the threefold size expansion of the human brain and its increased prefrontalization are most likely what allowed a symbolic language to evolve. Symbolic speech and gesture merge with other modes of communication, such as nonverbal and emotional

signals, but also remain separated by several degrees from nonlinguistic forms. Many other species have the capacity to communicate nonverbally and through vocal calls, but these systems are often viewed as qualitatively different from language because, among other things, they may only be elicited by immediate environmental cues and are involuntarily produced. (However, these points of view are becoming less fashionable in light of various findings reviewed below). Human language can be controlled voluntarily, can refer to past, present, and future events, and follows structural rules which combine a finite number of sound units into a potentially infinite array of sentences. Also, the combination of these units allows for the expression of thought and symbolic reference. Thus meaning is expressed in human languages which, according to some (Deacon, 1997), represents the widest chasm separating human language from nonhuman communication.

The adaptive functions of various animal communication systems, such as calls associated with predators, food, and conspecific mating or competition, are perhaps easier to identify than for human language. It is difficult to imagine an evolutionary scenario wherein fitness advantages accrued to those capable of using symbolic reference; much more so than it is to recognize the adaptive function of mating calls. Many linguists consider language to be an innate feature of human cognition, but do not offer explanations as to what function(s) language serves. In contrast to this, Pinker (1994) and Pinker and Bloom (1992) consider the expression of complex thoughts, rich in meaning, to have been of adaptive value among early hominids, where cooperation, as well as cheater detection, were of great importance. As Pinker and Bloom (1992) state "...humans, probably early on, fell into a life-style that depended on extended cooperation for food, safety, nurturance, and reproductive opportunities" (p. 483). According to this view, language allowed for an unlimited expression of thought and those with at least rudiments of the capacity presumably found themselves at a reproductive advantage over those more inclined to simply grunt.

According to evolutionary psychological points of view, whatever the adaptive functions of symbolic language, be it for cooperation, social manipulation, etc., the advantage was bestowed upon its users during the EEA. However, similar selective pressures for communication clearly existed prior to the EEA. Pre-hominid species presumably also "fell into" lifestyles where cooperation for food, safety, nurturance, and reproductive success were better attained by communicating. It is difficult to imagine these needs suddenly arose for

humans only during the EEA. While various features of language may be unique to humans, foundational components such as meaning and intentionality are present in the communication of other extant species. It is these capacities upon which a significant part of human language may have been built. Therefore, a time period and setting different from the EEA might be a better place to look to discover the evolutionary origins of language.

Those who take a hard-line view of language definitions tend to define language in ways that disqualify nonhuman communication as comparable (e.g., Bickerton, 1998; Pinker, 1994). Many comparative psychologists, on the other hand, view human language as built upon a mental substrate existing among nonhuman species (mostly primates). The use of grammar, for example, is often considered an ability that evolved along the hominid lineage with no comparable ability to be found among primate vocalizations. However, Savage-Rumbaugh et al. (1993) found that a bonobo chimpanzee making use of lexigram symbols was capable of generalizing syntactical rules to novel situations and grasped differences in meaning due to changes in the grammatical structure of sentences. Reference, meaning, and intentionality are present in many primate calls. That these communicative properties are present supports the view that several aspects of human language are built upon abilities originating prior to the origin of the hominid line.

Ape language research has been largely ignored (and criticized) by several evolutionary psychologists (Bickerton, 1998; Pinker & Bloom, 1992; Plotkin, 1998). Apes taught to use gestural signs or artificial languages have revealed some similarities between human and nonhuman language, yet many differences remain. However, the existing similarities should not be summarily dismissed. They require careful examination if the aim is to trace the evolutionary history of human language, especially when there is consideration of the mental abilities necessary for it, and the selective pressures that influenced them. Plotkin (1998) asserts that "What the ape language studies do seem to share with experiments on the likes of 'mind-reading' and 'self-awareness' in other apes is a prejudiced stance among many primatologists who want to see such 'upper'-level human cognitive abilities in other primates, and hence make inflated claims for what their studies show" (p. 127). Such a view will not hasten the progress that can be made in tracing the evolution of language. Conversely, the unwillingness on the part of many to take into account nonhuman primate research leads to inflated claims about the uniqueness of human

language. The results of ape-language projects are indeed germane to the question of language origins. However, evaluating the selective pressures and functions associated with language evolution may best be done from a more naturalistic perspective. Regardless of what ape-language studies have or have not told us about human language, a more applicable approach to the subject comes from ethological research on animal communication.

THE ETHOLOGY OF REFERENCE

Reference is one aspect of human language that is shared with nonhuman species. Reference can take a variety of increasingly complex forms: mimetic, proxy, and conceptual (Allen & Saidel, 1998). Mimetic reference occurs when a response is elicited by a stimulus that resembles the referent. For example, angler fish attempt to lure prey by "mimicking" food typically eaten by their own unsuspecting prey. This is not a "higher-level" of reference because no intentionality is necessary on the part of the signaler and the signal is in no way arbitrary with respect to the context (see below for further discussion on intentionality). A proxy referential signal elicits the same response as the actual referent itself (Allen & Saidel, 1998). The anti-predator alarm calls of many bird, rodent, and primate species are proxy referential in that they may refer to a particular predator, and the signal is perceptually paired with the stimulus. Conceptual reference is the most stimulus-removed of the three forms of referential communication, and occurs when a signal refers to something external with no expectation of a response that is normally evoked by the referent. When we speak of objects or events that are not immediately present we are using conceptual reference.

Proxy reference is probably the most ubiquitous form of referential communication found among nonhuman organisms, although evidence for conceptual reference does exist among language-trained apes. The alarm calls of vervet monkeys (*Cercopithecus aethiops*) are considered to be proxy referential. Specific calls are produced in response to certain predators (snakes, eagles, and leopards). These monkeys also emit different calls when they move into open areas, when encountering another monkey troop, and during aggressive interactions with conspecifics. Cheney and Seyfarth (1988) consider these calls to have meaning to vervets, and that they respond to the calls based on the semantic differences that are reflective of the discreteness of the calls

(see below). These vocalizations are not hard-wired from birth, but rather follow a developmental course relying on both maturational and experiential factors (Hauser, 1989; Seyfarth & Cheney, 1986). Vervet monkeys must learn to discriminate both among and within different predator types. Young vervet monkeys, for example, emit calls for aerial predators when the stimulus might actually be a non-threatening bird; but this response is eventually extinguished. Vervet monkeys also appear capable of recognizing the calls of individual group members, and are sensitive to the reliability of an individual's calls within referent categories (e.g., predators vs. conspecifics).

Proxy reference requires an element of shared attention. If the signal is an alarm call, the recipient may simply look in the vicinity of the caller in an attempt to discover the specific location of the predator. Or, the recipient may look in the direction toward which the caller is looking. This has not been experimentally manipulated in field settings (but see Cheney & Seyfarth, 1982), but several nonhuman primate species evince the capacity to follow gaze directions of humans or conspecifics in laboratory experiments (Emery, et al., 1997; Povinelli & Eddy, 1996; Tomasello, Call, & Hare, 1998). Joint visual attention, an advanced form of gaze following, is thought to facilitate the development of language in human infants (Bruner, 1983; Goldfield, 1990). Captive chimpanzees with various rearing histories engage humans in bouts of joint attention when communicating the location of objects by pointing (Krause & Fouts, 1997; Leavens & Hopkins, 1998). However, this appears to serve an imperative function and differs from the declarative pointing often seen in human infants, which functions to show objects and events to others. Regardless, the requisite behaviors for shared attention are present in both human and nonhuman, and their relationship to language acquisition in the former is indeed critical. Humans have expanded upon this capacity by engaging in joint visual attention as a mode of acquiring vocabularies. However, the selective pressures for engaging in shared attention in primates, at least, existed prior to the hominid split. From a developmental perspective, the evolution of human language owes much to the ability to engage in joint visual attention.

CATEGORICAL PERCEPTION OF SPEECH AND SOUND

Speech comprehension requires that the listener is capable of categorically discriminating phonemes. For humans as well as

nonhumans, categorical perception of non-phonemic sounds also occurs. Macaques, chinchillas, sparrows, and mice all show evidence for categorical perception of speech sounds as well as of sounds made by conspecifics (see Evans & Marler, 1995 for review). Therefore, the capacity to receive and categorize auditory stimuli, a fundamental requirement for the comprehension of speech, preceded the evolutionary onset of speech. Similar to speech, vocal call perception is lateralized to the left hemisphere in many mammalian and avian species (see Hauser, 1996 for review). Therefore, the neural adaptations for vocal processing may be phylogenetically ancient. Vervet monkeys are capable of categorizing alarm calls, but the meaning these calls may have to the animals is a different issue. Whether animals base their responses to vocalizations on meaning has further implications for the evolution of language.

MEANING AND PRIMATE VOCALIZATIONS

Cheney and Seyfarth (1988) correctly maintain that "Humans make judgments about the similarity or differences between words on the basis of an abstraction, their meaning" (p. 477). Cheney and Seyfarth (1988) reasoned that if two vervet monkey calls have similar meanings, monkeys should transfer habituation from one played-back call to another if the initial call comes from an unreliable monkey (that is, no observable referent is present when the call is played). Their results suggest that indeed vervet monkeys judge the relationship between calls based on meaning. Their habituation to one type of aggressive call transferred to another type of aggressive call made by the same (unreliable) monkey. Therefore, vervet monkeys may classify physically dissimilar calls into meaningful categories. The ability to assess calls based on meaning by nonhuman organisms suggests that the requisite cognitive capacities existed prior to the origin of hominids.

Syntax makes human language perhaps the most complex, and the least constrained, of all animal communication systems. The devices and rules used to convey meaning make for an infinite level of productivity and are among the hallmarks of human languages. Did the intense need for cooperation and nurturance result in selection for an original, infinitely productive grammatical language? Selection for the ability to use syntax was potentially quite strong during the EEA. However, this may have been built upon more ancient abilities that existed prior to Hominids. According to Mitani and Marler (1989),

male gibbon songs vary by duration, frequency range, minimum and maximum frequency, start and end frequency, and inflection. Similar types of call variation in chimpanzees and bonobos exist as well (Hohmann & Fruth, 1994; Mitani, Hasegawa, Gros-Louis, & Marler, 1992). Although simplistic and motivationally limited, many primate vocalizations involve the combination of various elements that potentially vary in meaning according to their structure. Whether primate calls have anything remotely similar to syntax remains to be firmly established.

INTENTIONAL COMMUNICATION

Whether primates mean to signal is a separate issue from whether their signals have meaning. Neurological studies of animal communication systems frequently show that more ancestral brain regions control vocal behavior. It follows from this that primate calls, for example, are only evoked by the presence of certain stimuli and motivational states, and are not under voluntary control. The fact that vervet monkeys use referential calls and appear to understand the meaning of these calls is suggestive of intentionality, but is not unequivocal evidence for it. Tomasello and Call (1997) offer two additional criteria for distinguishing intentional from non-intentional communication - "flexibility of use and use in socially sensitive ways (i.e., audience effects)" (p. 252). As previously noted, the ontogeny of vervet alarm calls is somewhat flexible. Although young vervet alarm calls are acoustically adult-like, their appropriate usage is largely based on experience. Anecdotal evidence also suggests that vervet monkeys use their calls deceptively, but this may be a type of "functional" deception, rather than "tactical" deception (Cheney & Seyfarth, 1990), which requires the attribution of false beliefs.

The presence of conspecifics may determine whether vervet monkeys, and even squirrels (Sherman, 1977), and chickens, vocalize. Vervet monkeys typically do not alarm call unless others are close by (Cheney & Seyfarth, 1990). Similarly, the humble domestic chicken is more likely to emit predator alarm calls when in the vicinity of hens, than when quail or an empty cage are nearby (see Evans & Marler, 1995 for review). While these results should be interpreted with caution, they may indicate that various animal vocalizations are controlled voluntarily. The gestural communication of great apes shows much stronger evidence of intentional communication among

nonhuman organisms. However, most of these studies are conducted in laboratories under controlled experimental conditions. Often these subjects have had extensive contact with human caregivers, which, although informative in many ways, compromises their ethological validity (see Tomasello & Call, 1997 for review and extensive discussion). Regardless, there is strong evidence for intentional communication among captive apes, and although it may not be regularly expressed in the same variety of ways in natural situations, support is lent to the notion that communication could be done intentionally prior to the hominid line.

THE COMPARATIVE METHOD AND COMMUNICATION

The comparative method has become a very useful tool for examining the phylogeny of behavior (Burghardt & Gittleman, 1990; Martins, 1996). The comparative method could be well applied to studies of human and nonhuman communication, and could provide a systematic way of identifying the fundamental similarities and differences between animal communication systems. Extensive treatments of the evolution of language that include comparative psychological viewpoints can be found in Velichkovsky and Rumbaugh (1996) and Krasnegor, Rumbaugh, Schiefelbusch, and Studdert-Kennedy (1991).

Jolly (1972) and Parker and Gibson (1979, 1990) originated the field of Comparative Developmental Evolutionary Psychology (CDEP). Comparative studies of language are one focal point of this approach. In addition to this, the non-linguistic, cognitive development of humans and nonhuman primates are treated as amenable to comparison; an approach that dates at least back to James Mark Baldwin's (1894) initial speculations and empirical studies. Based on their early review and initial model derived from comparative data, Parker and Gibson (1979) conclude that the common ancestor of humans and great apes "...displayed rudimentary forms of late sensorimotor and early preoperational intelligence similar to that of one- to four-year-old children" (p. 367). Based on Parker (1996) and Parker and Gibson (1979), there is a trend toward greater sensorimotor complexity as the hominid line is reached. Cognitive development has not been a major focus of evolutionary psychological research thus far, but the field will be better informed if results from CDEP studies are considered and the comparative method used. This will also require practitioners to loosen

the theoretical confinement posed by the EEA concept.

Evidence for categorical perception of speech, reference, meaning, and intentionality exists in several nonhuman communication systems (Allen & Bekoff, 1997; Hauser, 1996). This has potentially significant implications for the evolution of human language. A complex system like human language can and should be broken down into the elements that comprise it. The main point here concerns which of these elements existed prior to the hominid line. The EEA may be too simplistic and confining as a concept that can adequately reflect the complexity of the origins and evolution of language and human cognition. I second Daly and Wilson's (1995) assertion that "Comparative evidence can ...aid us in better characterizing the adaptive functions of particular attributes in a focal species, such as *Homo sapiens*" (p. 37).

CONCLUSION

Thus far I have not dealt much with how the behavioral comparisons made above corroborate with neuroanatomical characteristics of human and nonhuman brains. The cortical representation of language in humans, and in that of nonhuman communication systems, have previously been compared in the attempt to determine whether language has an evolutionary basis in homologous brain regions of other species (Deacon, 1991). The vocalizations of well studied species such as squirrel monkeys and macaques are largely controlled by the midbrain, diencephalon and limbic regions (Deacon, 1991). The perception of vocal signals, however, occurs in higher cortical regions of nonhuman primate brains (Rauschecker, Tian, & Hauser, 1995). One challenge to comparative neuroanatomists is to discover the neural units that give rise to specific aspects of language and communication that humans and nonhuman animals share. The edited volume by Steklis and Raleigh (1979) and Hauser's (1996) *Evolution of Communication* review much of the work done in this area.

The modular model of the brain has been incorporated into much evolutionary psychological theory. The applicability of this model to many psychological processes is potentially extensive. However, the original application of Fodor's (1983) "Modularity of the Mind" was specific to human language (and somewhat to visual perception). Evolutionary psychologists might overextend this model and infer the existence of modules for nearly every thought process and behavior

studied. The appeal of the modular brain model is clear, as it offers a material on which selection can act that is both unitary in function, yet integrated within the nervous system. However, it is important to remember that both evolutionary and comparative psychologists are typically measuring behavior and thought processes, and not modules per se. The existence of modules themselves is based on inference. This is not necessarily misleading, but it seems important to resist allowing the proverbial tail to wag the dog.

Some evolutionary psychologists imply that language is adaptive by virtue of its vast complexity (Pinker & Bloom, 1992). In other words, why would something so complex evolve if it had no adaptive value? I am in agreement with this position. However, this does not explain what language is adapted for or why it originated. As previously mentioned, Pinker and Bloom (1992) consider the unlimited expression of thought facilitated by language to be crucial to developing cooperation among its users. Furthermore, according to this view, language is a fairly recent phenomenon that originated among Pleistocene hominids. In examining the origins of language with greater accuracy, it seems necessary to specify which Pleistocene hominids were the adaptive language users (and was there only one EEA?). Potts' (1996) discussion on EEA related topics is a great source to consult for descriptions of ancestral environments, and it suggests that there was tremendous environmental variability encountered by human groups during this time. Finally, the notion that language evolved under selection pressures for communicating and cooperating with others seems much too general. Richardson (1996) has made a similar point, and discusses various criteria that should be implemented when an evolutionary explanation for an adaptation is needed. Among these criteria is that an independently established phylogeny should be used so that convergent and shared characters are recognized.

Applying evolutionary theory to human behavior is a step toward theoretical synthesis - a much-needed direction toward a unified psychology. The comparative method is a powerful tool that can aid evolutionary psychologists in identifying the origins of many other behavioral and cognitive traits. This method might require that some traits be broken down into constituent elements in order to map out their phylogenetic distribution. In addition, it could add scientific rigor to evolutionary psychology, and can circumvent some of the problems associated with assuming that human psychology is a product of selective factors that existed only during the EEA. The collaborative work of evolutionary and comparative psychologists and ethologists

should prove mutually beneficial, and in the end may provide a more accurate view of our own evolutionary past.

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